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Acanthodian dental elements from the Trundle beds (Lower Devonian) of New South Wales

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Abstract – Acanthodian dental elements from the Trundle beds (Lochkovian-Pragian) of central New South Wales include dentigerous jaw bone fragments, tooth whorls, single teeth, and dentition cones *sensu* Valiukevičius. Among acanthodians, only members of the Order Ischnacanthida possess an equivalent range of dental elements. Comparisons suggest that most of the Trundle beds elements belong to an ischnacanthid taxon with close affinity to *Poracanthodes*. Some other elements, distinctive tooth whorls including a type not previously described, possibly belong to a species with dentition that matches no known climatiid or ischnacanthid.

INTRODUCTION

The Class Acanthodii, as defined by recent workers (e.g., Denison 1979; Long 1986), has two orders which possessed teeth – the Climatiida and the Ischnacanthida. Amongst the climatiids, only fish of the family Climatiidae had teeth, comprising rows of tooth whorls. The Ischnacanthida are distinguished from other acanthodians by possessing dentigerous jaw bones, or gnathals, on both upper and lower jaws.

Acanthodian dental elements, including dentigerous jaw bone fragments, tooth whorls, isolated single teeth and dentition cones (*sensu* Valiukevičius 1992) occur in shallow water, marine limestones from the upper Lochkovian/lower Pragian Trundle beds (informal geological name; Pickett 1992; Pickett and McClatchie 1991) of central New South Wales (Figure 1). Isolated scales of at least four acanthodian species (Burrow in press) have been reported from these same beds. This material comprises rare scales of the climatiid *Nostolepis striata* and *Machaeracanthus* sp. (Acanthodii incertae sedis), and abundant scales of a new species (Burrow in press) and *"Nostolepis" guangxiensis* Wang, both of which might be ischnacanthids.

Few systematic descriptions of Australian Early Devonian acanthodian microremains have been published; Gross (1971a) described a small collection of acanthodian scales from Wilson's Cliffs, Western Australia, but the paucity and poor preservation of the material precluded classifying the scales. Long (1986) described small ischnacanthid gnathal bones of two types from the Emsian Spirifer yassensis and Cavan Bluff Limestones, Murrimbidgee Group, near Taemas, New South Wales, and from the uppermost Emsian Rocky Camp member, Murrindal Limestone, Buchan Group of Victoria. He assigned the bones to two separate genera, *Taemasacanthus* and *Rockycampacanthus* (Figure 2A–C) respectively. Turner (e.g., 1991) has recorded many occurrences of acanthodian scales, and has also reported occurrences of dental elements (e.g., Turner 1991, plate 2, fig. D).

Worldwide, a number of ischnacanthid taxa have been described based on isolated dentigerous jaw bones; only a small number (*Ischnacanthus gracilis*, *Uraniacanthus spinosus* and *Poracanthodes menneri*) are based on descriptions of articulated fish. Assigning the gnathal bones to the upper or lower jaw is often not possible, as only rarely is the posterior end preserved with the dentigerous area. Moreover, in the taxa based on articulated specimens, the upper and lower dentigerous zones are identical.

The present paper describes the acanthodian dental elements found in the Trundle beds samples, including two previously undescribed elements – a denticulated plate plus toothwhorl, and the posterior end of a probable upper jaw gnathal. An attempt is made to elucidate the dental patterns of the acanthodian fish from which the elements derive, and the affinities of these taxa are discussed.

MATERIAL

The specimens described in this study are from limestone samples collected and treated with acetic acid by Dr John Pickett (Geological Survey of New South Wales), and subsequently picked for microvertebrates by Dr Susan Turner (Queensland Museum) and the author. The samples are from

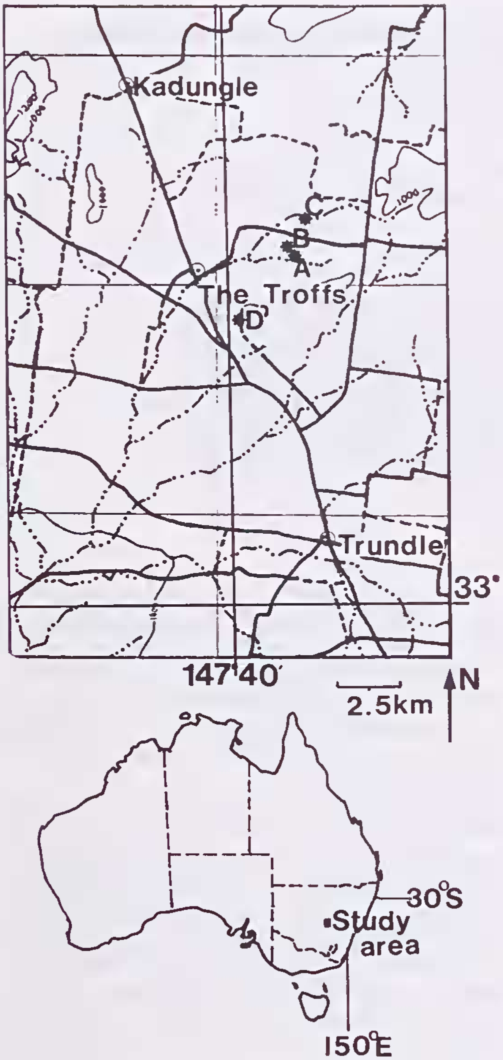

Figure 1 Location of sites C607, C661, C662 and C665 of the Trundle beds; map adapted from Australian Topographical Map Series 1:250000 Narromine. Site C607(=A): 6 km E of The Troffs railway station, GR 573500 941800; site C661(=B): tank S of "The Troffs" station, GR 573ooo 942ooo; site C662(=C): Dam at foot of hills of volcanics, "The Troffs" station, GR 575ooo 943ooo; site C665(=D): 3 km SE of The Troffs railway station, GR 572ooo 938ooo.

sites C607, C661, C662 and C665 in the Trundle beds of central New South Wales of Early Devonian age (Lochkovian; *pesavis* zone) (Table 1). Site and specimen numbers were provided by Dr Pickett; MMMC = Fossil collection of the Mineralogical and Mining Museum, Sydney.

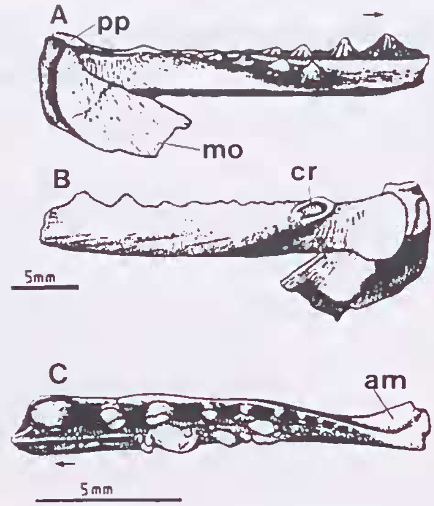

Figure 2 Gnathal bones of other Australian ischnacanthids, after Long 1986, figs 3A,C and B. A, *Taemasacanthus* lower jaw, medial view; B, same jaw, lateral view; C, *Rockycampacanthus* lower jaw, occlusal view. am = attachment area for adductor mandibulae, cr = circular ridge, mo = Meckelian ossification, pp = posterodorsal process of lower jaw. Scale bar = 5 mm; arrows indicate rostral direction.

DESCRIPTIONS

Class Acanthodii

Order Ischnacanthida Berg, 1940

Ischnacanthid fam., gen. et sp. indet.

Represented by 12 dentigerous jaw fragments, 21 tooth whorls, 14 isolated teeth, and 15 dentition cones (Table 1). In the following account the most

Table 1 Number of dental elements present in each Trundle beds sample.

	C607	C661	C662	C665
Anterior jaw fragment	3	4	–	–
Mid jaw fragment	–	3	–	–
Posterior jaw fragment	–	2	–	–
Symmetrical tooth whorl	5	8	–	–
Single tooth	7	5	2	–
Dentition cone I	5	2	–	–
Dentition cone II	5	2	–	1
Asymmetrical tooth whorl	1	–	–	–
Denticulated plate plus tooth whorl	1	3	2	1

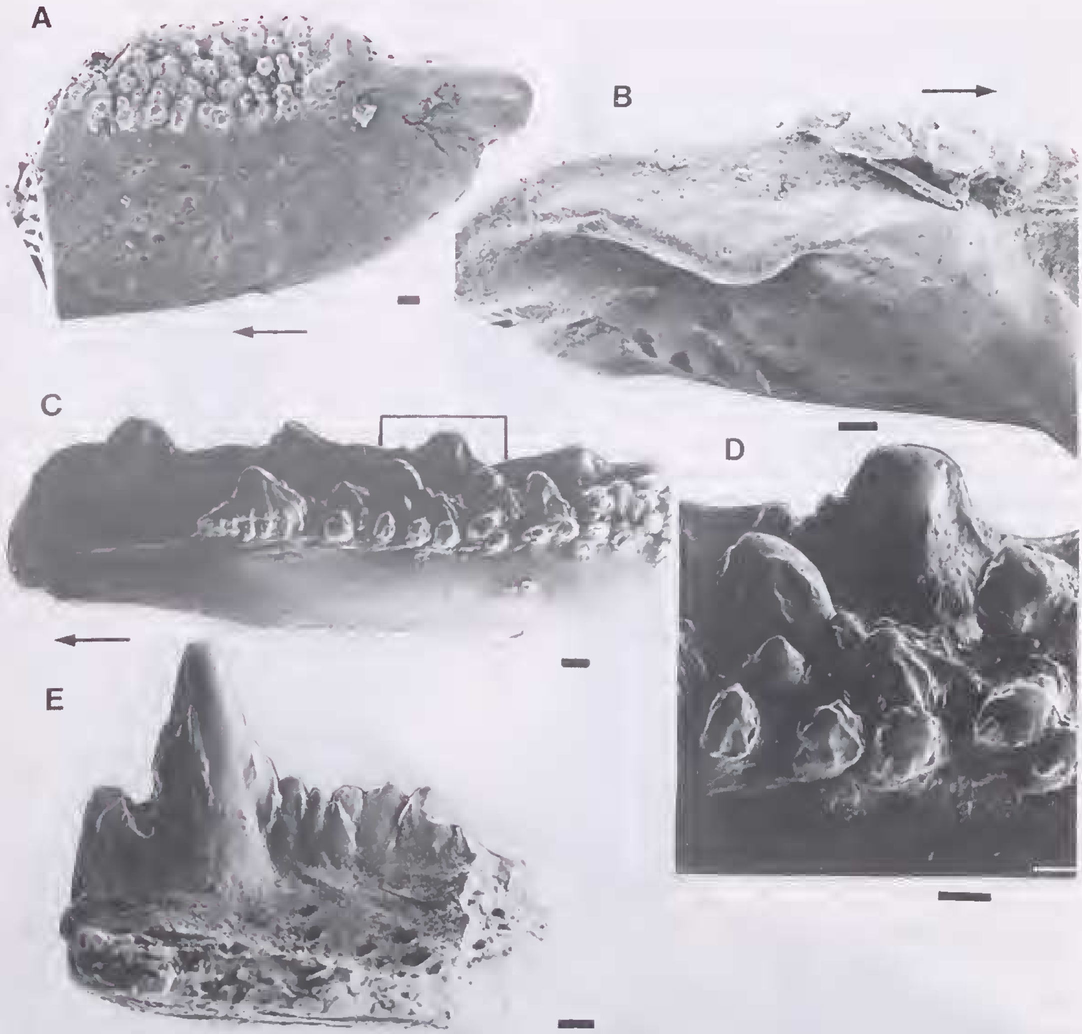

Figure 3 Dentigerous jawbone fragments from Trundle beds, central New South Wales. A,B, posterior ?upper jaw fragment MMMC02280: A, lateral view and B, occlusal/medial view; C,D, mid jaw fragment MMMC02279: C, medial view, D, close-up of tubercles on medial ridge in C; E, anterior jaw fragment MMMC02278. Scale bars = 0.1 mm; arrows indicate rostral direction; Figures C,D,E are SEM photographs of uncoated specimens.

complete or best preserved specimen of each type is first described and figured, followed by brief details of other specimens of the same type.

Posterior jaw bone fragment (Figure 3A,B)

This fragment (MMMC02280) is 2.4 mm long, 1.5 mm deep and 1.0 mm wide at the anterior, broken edge. The top edge of the bone is narrow, and the anterior section bears small rounded denticles. A small, flat, ledge-like process juts out medially towards the posterior end; the end of the bone then curves gently round to the bottom edge. On the medial side, a ridge starts at the anterior edge of the ledge-like process, increasing in size as it sweeps down and forward to form the medial side of the basal concavity for the jaw cartilage. The lateral side of the bone is slightly convex top to bottom, and bears small, rounded denticles in the upper half.

A second similar fragment is 3.0 mm long, with the same shape and relative robustness, and is contralateral to the illustrated jaw fragment.

Dentigerous jaw bone (Figure 3C,D)

The best preserved jaw bone fragment (MMMC02279) is 4.0 mm long, 0.7 mm wide posteriorly and increasing to 1.0 mm wide anteriorly, and is approximately 1.0 mm deep. The anterior and posterior ends are broken; the base is transversely concave. The main tooth row extends along the lateral edge of the occlusal surface of the jawbone, and comprises a series of five multicuspidate teeth which increase in size and number of side cusps posterior to anterior. The main cusps are sub-triangular in parabasal section, with the 'angles' positioned anteriorly, posteriorly and medially. The posterior teeth are low and worn, with side cusps barely discernible. The anterior teeth are formed by a main cusp and one medial, three anterior and two or three posterior cusps. The main tooth row is separated by a deep channel from a medial tuberculated ridge, which bears approximately 40 irregularly clustered tubercles varying from less than 0.1 mm wide to 0.5 mm wide at the base, and with from five to 13 or more radiating ribs. They have worn, rounded apices, and are directed medially or vertically. The ridge diminishes in height from 0.8 mm posteriorly to 0.4 mm at the anterior limit of the tubercles.

The other two fragments are shorter, but of comparable depth and robustness. If all three fragments had originally been positioned on the lower jaw, two are from the left side and one from the right side. A vertical, transverse, ground thin section was made of one of the fragments (MMMC02276, Figure 6A). Wide, vascular canals extend throughout the bone base, and up into the main cusp. Denteons surround some of the canals, with bone cell lacunae between the denteons. Orthodentine tubules are present in the large tubercle of the medial ridge, and in the upper section of the main tooth cusp.

Anterior jaw fragment (Figure 3E)

This fragment (MMMC02278) is 1.5 mm long, and has one almost complete tooth 'group' (i.e., a main cusp plus side cusps) with one large cusp, three posterior side cusps and two anterior side cusps. The distal surface of the jaw fragment is flat. The posterior cusps are overlapped laterally by the anterior cusps of the next tooth group. The main cusp is 0.6 mm high with a sub-triangular parabasal section, and the smaller cusps are about 0.15 mm high, and laterally flattened with an elliptical parabasal section.

The other six fragments range from 1.4 to 2.0 mm long, including a very robust fragment with a main cusp that is 2.0 mm high. It is not possible to determine the original orientation of most of the fragments. Figure 6B is of a vertical, longitudinal, ground thin section of a fragment (MMMC02274) with one main cusp and three side cusps, and illustrates the highly vascular structure of the bone base and main cusp. The secondary cusps are less vascular, and are formed of a relatively dense, dentinous tissue. Separation between the lateral ridge tissue and the central tissue of the main cusp is clearly delineated.

Symmetrical tooth whorl (Figure 4A)

In crown view, the base of this specimen (MMMC02249) is sub-triangular in outline, being 0.7 mm wide posteriorly and narrowing to a rounded point anteriorly. The base is arched, and is concave anterior to posterior. The crown has four tooth rows, with the cusps decreasing in size to the front. Each row has a prominent central cusp, the largest being 0.5 mm high; on each side there are up to four subsidiary cusps, approximately a quarter of the height of the central cusp. The central, or main, cusps have sub-triangular parabasal sections, with the angles pointing anteriorly and laterally. The three ridges which contribute to this triangular cross section differ in appearance from the central cusp area, being coloured white whereas the rest of the cusp is amber.

The other 12 tooth whorls of this type range greatly in size and relative robustness of the cusps and base: the smallest is 0.4 mm long and high, while the largest is over 2.0 mm long with a central cusp nearly 2.0 mm high. The tooth whorls comprise from three to six tooth rows; on some, the main cusp is only about twice as high as the side cusps, while on others the main cusp is up to four times as high (e.g., toothwhorl MMMC02256, Figure 4B,C). The number of cusps per tooth row is also variable, with from two to six or more side cusps. The number of side cusps varies independently of the size of the tooth whorl. One of the tooth whorls (MMMC01962, Figure 4G), while having the same generalized form as the other tooth whorls in this category, has a 'segmented' base corresponding to its tooth rows. In Figure 6C, a vertical, rostro-caudal, ground thin section of tooth whorl MMMC02275, central 'pulp canals' of the main tooth cusps are clearly visible, with fine orthodentine tubules radiating obliquely from them. Bone cell lacunae appear to be concentrated in the bone base.

Single tooth (Figure 5A)

The slightly recurved tooth (MMMC02277) is 0.7 mm high and has a base diameter of 0.3 mm. It has a narrow conical shape, with a hollow base of circular cross section, and a rounded apex. The tooth has a ring of small cusps approximately 0.4 mm from the tip, and has the dull appearance of bone below this ring, whereas it is shiny and dentinous above it.

The other 13 teeth are all of a similar size and shape.

Dentition cone, type I (Figure 5B)

This element (MMMC02252) is a hollow, thin-walled, bisymmetrical cone, 1.0 mm high, with a base diameter of 0.35 mm. It is characterised by an apex to base line of oblique spiny denticles. The

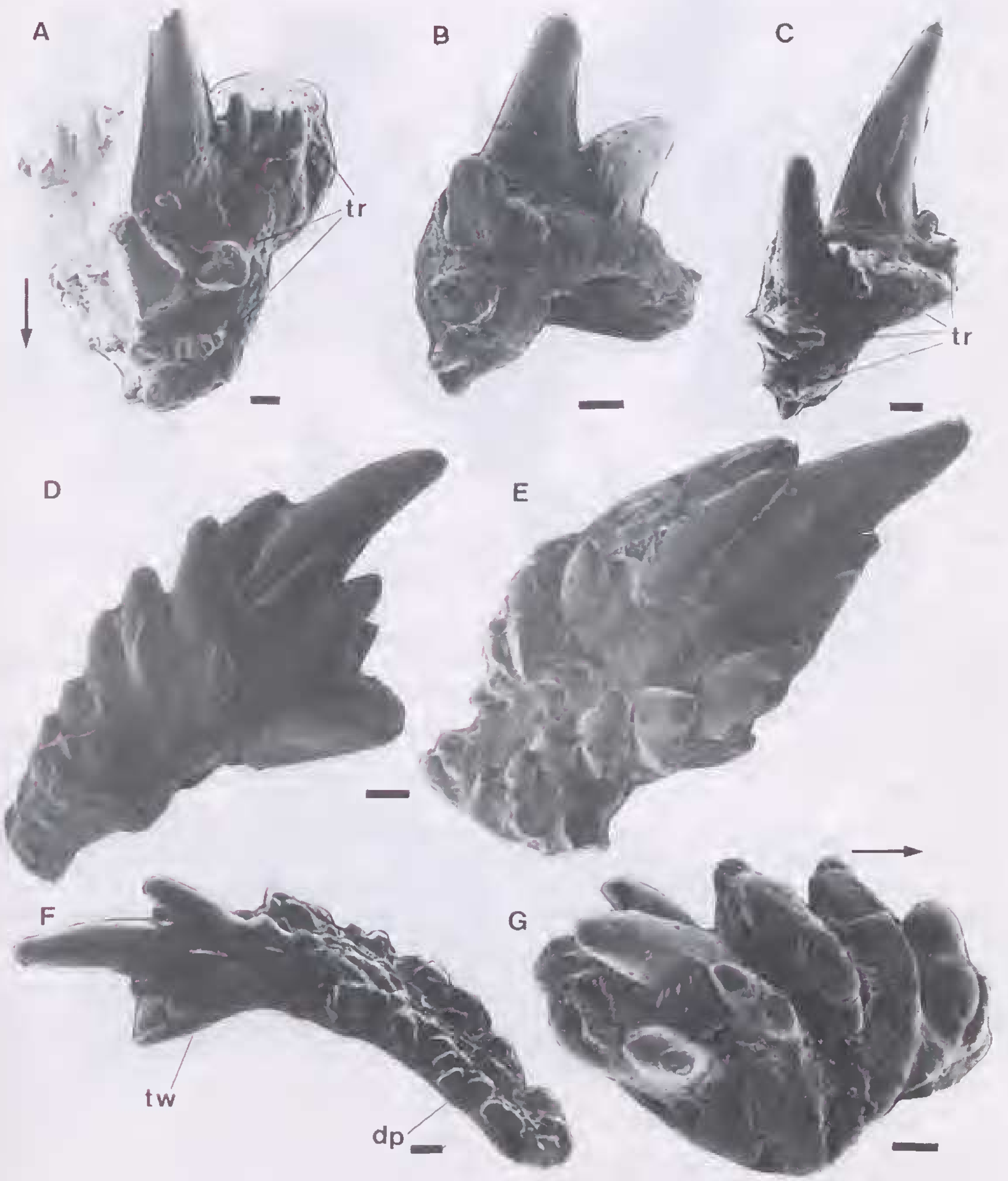

Figure 4 Tooth whorls from Trundle beds, central New South Wales. A, occlusal view, ischnacanthid symphysial tooth whorl MMMC02249; B,C, symphysial tooth whorl MMMC02256, with main central cusp ca. four times as high as side cusps: B, antero-lateral view, showing arched base, and C, occluso-lateral view; D, lateral view, and E, occlusal view of ?mouth cavity multiple tooth whorl MMMC02250; F, lateral view of denticulated plate plus tooth whorl MMMC02251; G, occluso-lateral view of symmetrical tooth whorl MMMC01962. dp = denticulated plate, tr = tooth rows, tw = tooth whorl. Scale bars = 0.1 mm; arrow indicates rostral direction; Figures A,D,E are SEM photographs of uncoated specimens.

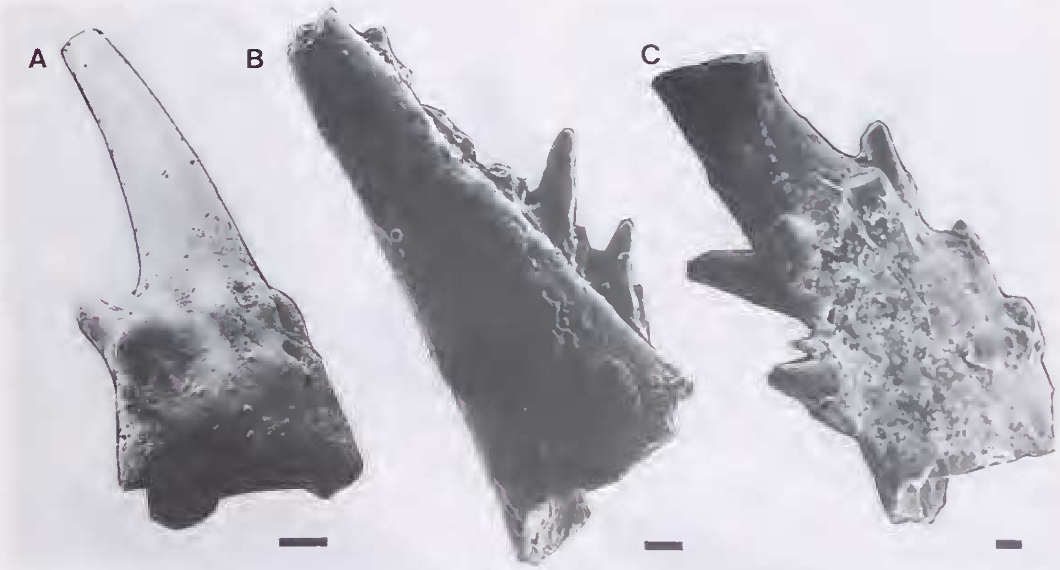

Figure 5 Single tooth and tooth-like cones from the Trundle beds, central New South Wales. A, single tooth MMMC02277; B, tooth-like cone type I MMMC02252; C, tooth-like cone type II MMMC02268. Scale bars = 0.1 mm; A is an SEM photograph of an uncoated specimen.

latter appear to consist of a row of tooth-like processes interspersed with smaller, irregularly arranged processes/cusplets. The arrangement is reminiscent of that of the main cusp row of the dentigerous jaw bones.

The other six cones of this type are of a similar size and shape.

Dentition cone, type II (Figure 5C)

This cone (MMMC02268) is more robust than the previous type, with thicker walls and oblique denticles scattered over the cone surface. The main cone body is formed of bone, while the denticles are shiny and probably dentinous.

The other six cones range from 0.8 to 2.0 mm high.

Class Acanthodii *incertae sedis*

Acanthodii gen. et sp. indet.

Asymmetrical multiple tooth whorl (Figure 4D,E)

This incomplete element (MMMC02250) is 0.9 mm long and 0.4 mm wide centrally, and has an arched base, bearing radiating whorls of teeth. The crown comprises two apparently complete whorls, each with at least six teeth or tooth rows. The teeth increase gradually in height from less than 0.1 mm at the front to as much as 0.6 mm at the rear. The largest tooth row of the best-developed whorl has the largest central cusp, which has two side cusps about 0.15 mm high. The cusps are sub-circular in parabasal section. Side cusps are poorly developed or absent on most teeth. Adjacent to the anterior section of this whorl are two broken teeth which appear to be part of a third whorl.

Denticulated plate with tooth whorl (Figure 4F)

This asymmetrical element (MMMC02251) is 1.1 mm long and 0.3 mm wide. The posterior portion has a similar form to that of typical tooth whorls – i.e., a concave base, and tooth rows with a large central cusp and smaller side cusps. The whorl is skewed relative to the anterior base plate, which is elongated and flat. Its crown has worn, irregularly shaped cusps or tubercles. The thin lateral edges of the plate are also tuberculated.

The other six plates are of a similar size and pattern; three have a tooth whorl skewed right relative to the plane of the plate, and three are skewed to the left (if all were originally positioned in either upper or lower jaws). Plate MMMC02205 (Figure 6D) was sectioned longitudinally; unfortunately, preservation was poor, and most histological detail is obscure (Figure 6E).

DISCUSSION

Early ischnacanthids possessed a wide range of dental elements, as evidenced by those fish that have been found as articulated specimens, and by the detailed studies of microremains by Gross (e.g., 1957, 1967, 1971b). In the following paragraphs, the new specimens are compared with those previously described, to determine the possible positions and affinities of the dental elements.

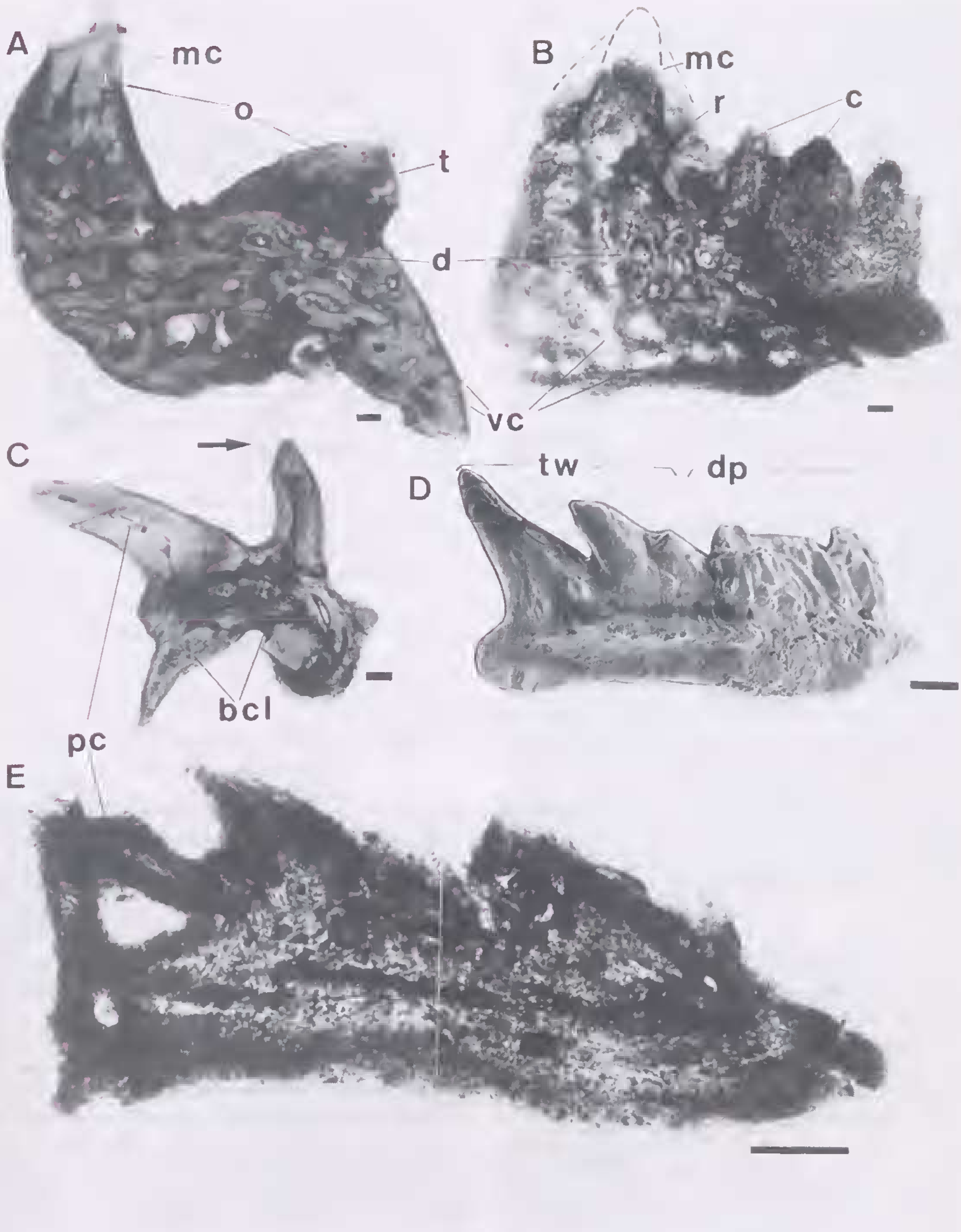

Figure 6 Ground thin sections of dental elements from the Trundle beds, central New South Wales. A, vertical transverse section of dentigerous jaw bone fragment MMMC02276; B, vertical longitudinal section through the main cusp and three side cusps of jaw bone fragment MMMC02274; C, vertical longitudinal section of symphysial tooth whorl MMMC02275; D, SEM photograph of uncoated denticulated plate with tooth whorl MMMC02205; E, longitudinal section of plate in D. bcl = bone cell lacunae, c = side or secondary cusps, d = denteon, dp = denticulated plate, mc = main cusp, o = orthodentine, pc = 'pulp' canal, r = lateral ridge of main cusp, t = tubercle of medial ridge, tw = tooth whorl, vc = vascular canal. Scale bars = 0.1 mm; arrow indicates rostral direction.

Gnathal bones

Ischnacanthid dentigerous jaw bones, and fragments thereof, are often readily recognizable by their characteristic latero-medially arched, basal concavity, which straddled the jaw cartilages. Ischnacanthids had the simplest jaw joint of all acanthodians, with a single simple articulation (Long 1986). In *Taemasacanthus* the lower jaw articulation area is on the end of a "meckelian ossification" (Long 1986, figure 3a), rather than the dentigerous jaw bone, and the posterior margin of the latter is splayed outwards. The posterior margins of lower jaw gnathals of *Persacanthus* (both in the holotype material, and a jaw described by Reed 1986), *Rockycampacanthus* (Long 1986) and *Atopacanthus* (Ørvig 1957, plate 2, figure 5) have a similar shape, and also lack any sign of an articulation area. Posterior jaw bone fragments comparable to those found in the Trundle beds were figured by Gross (1971b, plate 7, figures 1,13,14), and captioned as lower jaw fragments of *Nostolepis striata*, based on the erroneous assumptions that (a) *Nostolepis* lower jaws had dentigerous bones, while the upper jaws had rows of tooth whorls, and (b) that the elements were from *Nostolepis*, whereas they are probably from *Poracanthodes* (this misconception is further elaborated in the next paragraph). Unfortunately, on most other ischnacanthid gnathals that have been described, any ossification of the cartilaginous jaw articulation areas is either not present or not preserved, and only rarely is the posterior end of the gnathal preserved intact. Reed (1986:415) proposed that some of the jawbones depicted by Ørvig (1957, plate 2, figures 1,2), which have an extra posterior "knob" could be from the upper jaw. However, there are no other features to distinguish them from `proven' lower jaw bones. Certainly, on all three jaws figured by Ørvig with preserved posterior ends, the latter are splayed outwards. By comparison with these known cases, it seems possible (if only because of the lack of features attributable to known lower jaw gnathals) that the posterior jaw fragments described in the present paper are from the upper jaw. This interpretation is supported by a comparison with the articulated jaws of *Poracanthodes menneri* figured by Valiukevičius (1992, plate 11, figure 1). Although the posterior jaw bone segment is not preserved, the palatoquadrate cartilage retains the impression of the shape of this bone (see Figure 7A), and this compares well to the `negative' of the `positive' posterior jaw fragment (Figure 3A). Also, the impression left by the posterior end of the lower jaw bone in this specimen is consistent with that expected for the known lower jaw type.

Gross (1957, 1971b) described two jaw bone types from the Late Silurian Beyrichienkalk as *Nostolepis*- and *Gomphonchus*-type. The Trundle beds jaw fragments (Figure 3C–F) are very similar to examples that were attributed by Gross (1971b, figure 9A–F) to *Nostolepis*, but which have since been removed to *Gomphonchus* (Denison 1976). As well as having a medial tuberculated ridge, the jaw bone described here has a similar arrangement of side cusps, with about three cusps both anterior and posterior to the main cusp in each tooth group. As noted by Denison (1976), the differences between the two types of jawbones may indicate that the two scale-based species to which he tentatively assigned them, *G. sandelensis* and *G. hoppei*, may not be congeneric. Indeed, following the validation of *Poracanthodes* as a distinct taxon by Valiukevičius' (1992) description of articulated specimens of *P. menneri*, it now seems the *Nostolepis*-type jaw bone belongs to *Poracanthodes*

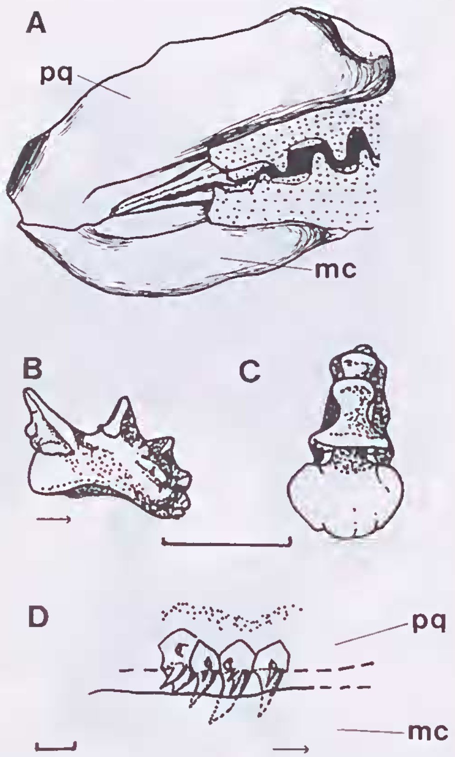

Figure 7 Articulated jaws of *Poracanthodes menneri*, and climatiid tooth whorls. A, *P. menneri* right upper and lower jaws, after Valiukevičius 1991, plate II, fig. 1: preserved dentigerous gnathals stippled; B, lateralview and C, anterior view, of tooth whorl of *Nostolepis striata*, after Gross 1957, taf. 4, fig. 7b,c; D, *Latviacanthus*, showing four tooth whorls, after Schultze and Zidek 1982, fig. 3. mc = Meckelian cartilage, pq = palatoquadrate cartilage. Scale bars = 1.0 mm; arrow indicates rostral direction.

or to a closely related genus. This hypothesis is supported by the composition of residues from Late Silurian beds of Cornwallis Island, Arctic Canada (Sample Tc415[4+5], Tom Uyeno collection), in which the only acanthodian remains are large scales of *Poracanthodes* cf *P. porosus* co-occurring with jaw fragments of *Nostolepis*-type *sensu* Gross (personal observation). The occurrence of this type of jaw bone in the samples from Trundle beds, which have no *Poracanthodes* scales, but which do have scales of "*Nostolepis*" *guangxiensis* (Wang), resembling those called *Gomphonchus* cf *G. hoppei* by Vieth (1980), and scales of a new ischnacanthid (Burrow in press), suggest that *Poracanthodes* and one of these species are closely related.

Histological structure of the jaw bones is not readily of use in determining their affinities; Gross (1971b:27) recognized similar hard tissues in both *Gomphonchus* and "*Nostolepis*" tooth cusps, and wide variation in the development of vascular canals and denteons in "*Nostolepis*" jaw bones. Also Ørvig (1973:125) noted that the side cusps in both *Gomphonchus* and "*Nostolepis*" are formed of a similar dentinous tissue.

Jaw bone fragments similar to those described here have also been recorded from the Lower Devonian Obere Carazo Formation, Profil Arauz, of Palencia, Spain (figured as "Ischnacanthidae indet." by Mader 1986, plate 3, figures 15,17a–c).

Tooth whorls

By comparison with the lower jaw symphysial tooth whorls of articulated ischnacanthids, the symmetrical tooth whorls (e.g., Figure 4A) were probably positioned in the lower jaw symphysis. These tooth whorls are similar to those attributed to *Gomphonchus sandelensis* (Gross 1967), but most of them differ in having more side cusps (up to eight per tooth row). Similar tooth whorls have also been described from the Lower Devonian Nakaoling Formation ("Siegenian") and Yukiang Formation (early Emsian) in the Liujing area of Hengxian County, China, assigned to *Gomphonchus liujingensis* Wang 1992, a species described on the basis of scales and a tooth whorl. The cusps of the paratype tooth whorl figured by Wang (plate 3, figure 2a–c), have a circular parabasal section rather than the sub-triangular section of the Trundle beds symmetrical tooth whorl MMMC02249 (Figure 4A), and are conspecific with scales that have a pore canal system in the crown. As mentioned above, the robustness, size, and relative size and number of tooth cusps in the Trundle beds specimens is quite variable. Histological structure of these tooth whorls (e.g., Figure 6C) appears identical to that of "*Gomphodus*" tooth whorls as illustrated by Gross (1957, plate 3, figures F–H). While some of the Trundle beds tooth whorls have cusps with a sub-triangular parabasal section, others, which lack the distinctive ridges, have a circular parabasal section. The triangular shape of the bone base of the tooth whorls indicates they are ischnacanthid symphysial whorls, as climatiid tooth whorls have parallel sides (e.g., Figure 7B,C). However, the variation in the Trundle beds tooth whorls indicates they could have derived from more than one ischnacanthid species.

The multiple tooth whorl (MMMC02250, Figure 4D,E) appears comparable to the spiky 'hedgehog'-like tooth whorls in the mouth cavity of *Gomphonchus* (Gross 1957, plate 3, figures 1,4–6). The tooth whorls described by Gross have strongly spiralled bases, but the Trundle beds tooth whorl is incomplete. In other features – three tooth rows, smooth recurved teeth and gradual increase in tooth size anterior to posterior – they are similar. In all ischnacanthid genera described from articulated specimens the symphysial tooth whorl (where present) is positioned in the lower jaw. Several types of isolated jaw bones have been figured (e.g., "*Gomphodus*" in Gross 1957, and *Taemasacanthus* in Long 1986, fig. 4A,D) with a cusp-free anterior segment. Perhaps some genera had parasymphysial tooth whorls/tooth whorl complexes on, but not ankylosed to, the jaw bone or cartilage in a comparable position to the tooth plates of dipnoans, or the tooth whorls of other higher osteichthyans (e.g., onychodontids). In its shape and robustness the asymmetrical tooth whorl described here certainly bears comparison with such tooth plates. These similarities support the possibility that the element had a parasymphysial position; alternatively, it may have been a pharyngeal element.

Denticulated plates plus tooth whorl

These elements (Figures 4F, 6D,E) do not match any previously described dental elements. Mader (1986, plate 3, figure 6a,b) figured a tooth whorl from the Lower Devonian Obere Carazo Formation of Spain which appears morphologically intermediate between this tooth whorl type and the fragile 'Borstenplättchen' (i.e., bristle plates) which Gross (1971b) suggested may have been supported by the branchial arches. Mader made no suggestions regarding their original anatomical position. The asymmetry of the Trundle beds element type indicates that it was paired, and its worn tubercles suggest that it opposed another (possibly identical) dental element. It might originally have been positioned in the pharynx; however, if this element, and the multiple tooth whorl (MMMC02250) which has similar cusps, came from a different species to the rest of the described elements, there are other possibilities. The shape of the base, the denticles on the narrow edges, and the wear on the denticulated surface, could indicate that it was supported by the jaw cartilage itself.

Perhaps these elements represent a dentition intermediate between the climatiid pattern of rows of tooth whorls, and the denticulated jaw bones of ischnacanthids. Nearly all climatiid tooth whorls described to date (e.g., from *Nostolepis striata* and *Climatius reticulatus*, Figure 7B,C) have flattened, blade-like cusps attached to a concave base of relatively constant width. *Latviacanthus* Schultze & Zidek 1982 is an exception: the cusps have a circular parabasal section, but unlike other climatiids the tooth whorl base concavity is at right angles to the curvature of cusps. That is, the cusps are directed rostro-caudally rather than medially, as in all other described species (Figure 7D).

Single teeth and tooth-like cones

The single teeth (Figure 5A) from the Trundle beds are similar to those previously attributed to *Gomphonchus* (Gross 1957). However, Gross' 'Dornzähne' have a broad concave base, whereas those from the Trundle beds do not. These teeth may be ontogenetically 'young' versions of the robust Type II dentition cones.

The two types of dentition cones, although bearing some similarity to phosphatized arthropod jaw fragments, appear identical to the cones described by Valiukevičius (1992), from the oral cavity of *Poracanthodes menneri*. The fragile Type I cones were possibly associated with the branchial arches. Although Valiukevičius (1992) suggested that the Type II cones were similarly positioned, their robustness could indicate a position further forward in the mouth cavity.

Many of the diverse acanthodian dental elements from the Trundle beds might derive from a single ischnacanthid species, but it is probable that they are from at least two species. As noted above, a large number of acanthodian scales has also been retrieved from the Trundle beds samples (Burrow in press); most of them have been assigned to *"Nostolepis" guangxiensis* Wang 1992 and a new species. The latter appears to belong to a group of acanthodians whose scales have a poracanthodid-type histology, but lack pore canal openings on the crown surface. Juozas Valiukevičius (Lithuanian Geology Institute, Vilnius) has also studied acanthodian scales from late Lochkovian deposits of the Baltic states, with this type of histology (pers. comm.).

A distinctive feature of all the tooth whorls and the jaw fragments is the arrangement of their cusps, with each large central cusp usually being flanked by two or three smaller cusps. Although the newly described element, the denticulated plate plus tooth whorl, and the multiple tooth whorl have a similar cusp arrangement to the other

Figure 8 Hypothetical reconstruction of lower jaw of ischnacanthid from the Trundle beds, central New South Wales (individual elements not necessarily to scale). aj = anterior jaw bone fragment, gr = groove, mr = medial ridge, pt = palatine tooth, ws = symphysial tooth whorl; arrow indicates rostral direction.

whorls and jaw fragments, the cusps of the former two have a circular parabasal section rather than the tri-carinate, or sub-triangular form of the cusps of the symphysial tooth whorls and jaw fragments. In an attempt to reconstruct the original anatomical positions of the various dental elements, these two types are kept separate. The proposed lower jaw reconstruction of the ischnacanthid fam., gen. et sp. indet. presented here (Figure 8), matches the pattern observed for *Poracanthodes menneri* Valiukevičius (1992). It incorporates all types of dental elements recorded for the latter species except the small pharyngeal tooth whorl. However, as neither of the Australian sciotaxa to which the elements probably belonged are classifiable as *Poracanthodes*, the jaw fragments and associated elements from the Trundle beds cannot yet be assigned with any certainty to either taxa.

CONCLUSIONS

The range of dental elements present in the Lower Devonian Trundle beds samples from New South Wales incorporates all known elements of ischnacanthid dentition, but also probable posterior ends of upper jaw gnathals, and at least one new form – the denticulated plate plus tooth whorls. The latter elements are of interest as they represent a dentition form which does not fit readily into recognized climatiid or ischnacanthid patterns. If the posterior ends of jaw bones do derive from the upper jaw, as proposed, they represent a previously unrecognized difference between ischnacanthid upper and lower jaw bones. The presence of those dental elements which can be certainly attributed to ischnacanthid acanthodians should prove of value in classifying the isolated scales present in the same samples.

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REFERENCES

Burrow, C.J. (in press). Lower Devonian microvertebrate assemblages of marine sediments (*pesavis/sulcatus* conodont zones) from central New South Wales, Australia. *Modern Geology*.

Denison, R.H. (1976). Note on the dentigerous jawbones of Acanthodii. *Neues Jahrbuchs für Geologie und Paläontologie*, Monatsheft 1976: 395–399.

Denison, R.H. (1979). Acanthodii. *In* H-P. Schultze (ed.), *Handbook of Paleoichthyology* 5:1–62.

Gross, W. (1957). Mundzähne und Hautzähne der Acanthodier und Arthrodiren. *Palaeontographica Abt. A* **109**: 1–40.

Gross, W. (1967). Über das Gebiß der Acanthodier und Placodermen. *In* C. Patterson and P.H. Greenwood (eds.), *Fossil Vertebrates*, Zoological Journal of the Linnean Society of London **47**: 121–130.

Gross, W. (1971a). Unterdevonische Thelodontier- und Acanthodier-Schuppen aus Westaustralien. *Paläontologische Zeitschrift* **45**(3/4): 97–106.

Gross, W. (1971b). Downtonische und dittonische Acanthodier-Reste des Ostseegebietes. *Palaeontographica Abt. A* **136**: 1–82.

Janvier, P. (1977). Les poissons devoniens de l'Iran central et de l'Afghanistan. *Mémoires de la Société Géologique de France* 8: 277–289.

Long, J.A. (1986). New ischnacanthid acanthodians from the Early Devonian of Australia, with comments on acanthodian interrelationships. *Zoological Journal of the Linnean Society of London* **87**: 321–339.

Mader, H. (1986). Schuppen und Zähne von Acanthodiern und Elasmobranchiern aus dem Unter-Devon Spaniens (Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie* **28**: 1–59.

Ørvig, T. (1957). Notes on some Paleozoic lower vertebrates from Spitsbergen and North America. *Norsk Geologisk Tidsskrift* **37**: 285–353.

Ørvig, T. (1973). Acanthodian dentition and its bearing on the relationships of the group. *Palaeontographica Abt. A* **143**: 119–150.

Pickett, J.W. (1992). Review of selected Silurian and Devonian conodont assemblages from the Mineral Hill and Trundle area. NSW Geological Survey Palaeontological Report 92/1 (unpublished) (GS1992/024).

Pickett, J.W. and McClatchie, L. (1991). Age and relations of stratigraphic units in the Murda Syncline area. *Geological Survey of New South Wales Quarterly Notes* **85**: 9–32.

Reed, J.W. (1986). The acanthodian genera *Machaeracanthus* and *Persacanthus* from the Devonian of Red Hill, Nevada. *Géobios* **19**: 409–419.

Schultze, H-P. and Zidek, J. (1982). Ein primitiver Acanthodier (Pisces) aus dem Unterdevon Lettlands. *Paläontologische Zeitschrift* **56**: 95–105.

Valiukevičius, J.J. (1992). First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya. *In* E. Mark-Kurik (ed.), *Fossil Fishes as Living Animals*: 193–213. Academia 1, Academy of Sciences of Estonia, Tallinn.

Vieth, J. (1980). Thelodontier-, Akanthodier- und Elasmobranchier-Schuppen aus dem Unter-devon der Kanadischen Arktis (Agnatha, Pisces). *Göttinger Arbeiten zur Geologie und Paläontologie* **23**: 1–69.

Wang, N-Z. (1992). Microremains of agnathans and fishes from Lower Devonian of central Guangxi with correlation of Lower Devonian between central Guangxi and eastern Yunnan, South China. *Acta Palaeontologica Sinica* **31**: 298–307.

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